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Wood-inhabiting fungi with tight associations with other species have declined as a response to forest management

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Research on mutualistic and antagonistic networks, such as plant–pollinator and host–parasite networks, has shown that species interactions can influence and be influenced by the responses of species to environmental perturbations. Here we examine whether results obtained for directly observable networks generalize to more complex networks in which species interactions cannot be observed directly. As a case study, we consider data on the occurrences of 98 wood-inhabiting fungal species in managed and natural forests. We specifically ask if and how much the positions of wood-inhabiting fungal species within the interaction networks influence their responses to forest management. For this, we utilize a joint species distribution model that partitions variation in species occurrences among environmental (i.e. resource availability) and biotic (i.e. species-to-species associations) predictors. Our results indicate that in addition to the direct loss of resource-specialised species, forest management has indirect effects mediated through interactive associations. In particular, species with strong associative links to other species are especially sensitive to forest management.

One of the long-standing challenges in ecology is to understand the mechanisms that determine the assembly and dynamics of species communities at different spatio-temporal scales. Factors structuring communities at local and regional scales have been associated to dispersal, abiotic environmental variation and biotic interactions (Götzenberger et al. 2012), whereas biogeographical and historical processes are considered more determinant at continental scales (Morin 2011). Environmental perturbations such as habitat loss and fragmentation may have significant effects on community dynamics at all scales (Opdam and Wascher 2004).

Habitat loss and fragmentation are likely to modify the interactions among species (Tylianakis et al. 2008) and thus the mechanisms related to their coexistence (Nee and May 1992). Within ecological communities, some species are sensitive to habitat loss and fragmentation while others are tolerant or can even benefit from fragmentation effects. Species with specialized resource use and low colonization capability have been found to be more sensitive to habitat loss and fragmentation than species with generalist resource use and high colonization capacity (Henle et al. 2004). This is partly so because habitat fragmentation increases the relative amount of ephemeral and isolated habitats, which according to the competition–colonization theory benefits superior colonizers and inferior competitors, which tend to be species with a generalist resource use (Abrams 2006).

One central question in community ecology is whether the responses of species to environmental perturbations depend on their positions within interactive networks (Tylianakis et al. 2008, Araújo et al. 2011). How networks of ecological interactions influence the responses of species and communities to habitat fragmentation has been the focus of many recent modelling (Borrvall et al. 2000, Fortuna and Bascompte 2006, Dunne and Williams 2009) and empirical (Biesmeijer et al. 2006, Aizen et al. 2012) studies. Both kinds of studies have found that mutualistic networks are especially vulnerable to habitat disturbances, and that species with few tight links to other species are more vulnerable to secondary extinctions than species with many weak interactions.

Thus far, most studies have focused on simple antagonistic and mutualistic interaction networks in a simplified spatial context, whereas only few studies have evaluated the consequences of habitat fragmentation for more complex interaction networks and for a realistic spatial context (Gonzalez et al. 2011). Further, many of the recent modelling studies have been based on classifying species pairs into those that do or do not interact, rather than quantifying the population dynamical consequences of the strengths of the interactions (Borrvall et al. 2000, Fortuna and Bascompte 2006, Dunne and Williams 2009). Consequently, there is still a lack of both theoretical and empirical studies examining how the responses of species to environmental perturbations

generally depend on the structures of the interactive networks and on the environmental context (Tylianakis et al. 2008, Morales-Castilla et al. 2015).

Wood-inhabiting fungi are an interesting case study of a highly interactive and species-rich community that follows resource–consumer dynamics, where the resources are provided by decaying trees. Fungal species interact with each other directly and indirectly in a number of mutualistic and antagonistic ways, including competition for nutrients and space, facilitation and inhibition of growth through metabolite secretion and modification of the substrate, and parasitism (Heilmann-Clausen and Boddy 2005, Boddy et al. 2008, Pippola and Kotiranta 2008). Consequently, these communities cannot be classified in a clear-cut way to different trophic levels, and even less so to simple bipartite graphs which have been the starting point for many modelling studies. Wood-inhabiting fungal communities have been much influenced by forest management, which has increased fragmentation in forested landscapes and reduced the availability of dead wood, and thus the species richness of habitat specialist species (Laaksonen et al. 2008, Abrego and Salcedo 2013, 2014, Nordén et al. 2013). Apart of the direct loss of species through reduction of available resources, forest management also indirectly affects fungal communities by increasing the competitive pressure for the remaining resources (Thorn et al. 2016). However, it remains unknown how the positions of the species in the interactive networks among wood-inhabiting fungi influence their responses to forest management.

Wood-inhabiting fungal communities within a single dead wood unit can consist of mycelial networks of tens of species, from which only the most abundant ones are detectable as fruit bodies (Allmér et al. 2006, Kubartová et al. 2012, Ovaskainen et al. 2013, Ottosson et al. 2015). This issue has raised an ongoing debate on the validity of results derived from fruit body based surveys compared to molecular based surveys (Halme et al. 2012). While it is clear that the number of species detected by a molecular study is much greater than what can be detected by a fruit body study, comparative results from fruit body and molecular studies show that community level inferences (e.g. drivers behind variation in species richness or community composition) derived from these two data types are generally consistent (Fischer et al. 2012). Moreover, given that molecularly detected species are usually found also as fruit bodies from other dead wood units within distances of tens of meters from the focal unit, fruit body surveys can perform as well as molecular surveys for detecting wood-inhabiting fungal richness at larger spatial scales than resource units (Runnel et al. 2015).

We acquired fruiting fungal occurrence data on ca 22 500 dead wood pieces located in both managed and natural beech forests, and use these data to model the community of 98 species of fungi as a function of environmental covariates and interaction networks at three different spatial levels: forest sites, sampling plots within forests, and individual resource units. Our aims are 1) to examine how the positions of the species within the interaction networks relate to their ecological niches, 2) to quantify how much of the responses of the species to forest management can be explained by species-to-species interactions relative to the match between niche and resource availability, and 3) to test the hypothesis derived from theoretical and empirical studies that species with tight associations with other species are especially sensitive to forest management.

Material and methods

Data collection

The data used here are the same used in Abrego and Salcedo (2013, 2014) and Ovaskainen et al. (2016). Briefly, the inventories were conducted in 8 natural and 21 managed forest sites of Navarre, northern Spain. We surveyed in each forest site 5–10 randomly located 10×10 m sample plots, in total 230 plots. Each plot was visited once, from late September to early November in 2011 and 2012. In each plot all dead wood pieces (called henceforth resource units) larger than 0.2 cm in diameter were checked and the occurrences of all saproxylic macromycetes (fungi with visible fruit bodies) were recorded. Data on the diameter, length and decay class of all resource units were recorded, whether or not fruit bodies were present. Decay was classified into 5 classes using a modified form of the method of Renvall (1995). The data involves 22 460 resource units, out of which 3809 were located in natural forest sites and 18 651 in managed forest sites. The total number of species is 326, but we restrict the analyses here to those 98 species that occurred at least five times in the natural forest sites. The data are published in Abrego et al. (2016b).

Statistical analysis

We utilize here a joint species distribution model that we have previously fitted to the subset of the data from the natural forests (Ovaskainen et al. 2016). The model is a multivariate probit regression model where the response variable is the vector of presence–absences of all species in each resource unit. The regression part of the model accounts for the influence of environmental covariates (size and decay class of the resource unit), whereas a latent variable part models species co-occurrences at the spatial scales of resource units, plots and forest sites.

To describe the model mathematically, we denote the resource unit by the index $i = 1, \ldots, n$ and the species by the index $j = 1, \ldots, m$, where n is the number of resource units and m is the number of species. We denote the presence-absence data by y_{ij}, so that $y_{ij} = 1$ if the species j was found in resource unit i and otherwise $y_{ij} = 0$. Species occurrence is modelled as $y_{ij} = 1_{z_{ij} > 0}$, where the latent occurrence score z_{ij} is defined as

$$z_{ij} = L_{ij} + \varepsilon^{R}_{ij} + \varepsilon^{P}_{P(i)j} + \varepsilon^{F}_{F(i)j} + \in_{ij} \quad (1)$$

The linear predictor L_{ij} includes the regression part of the model as $L_{ij} = \sum_{k=1}^{q} x_{ik}\beta_{jk}$, where the covariates x_{ik} are the intercept ($x_{i1} = 1$) and the log-transformed volume (x_{i2}), decay class (x_{i3}) and squared decay class (x_{i4}) of the resource unit, and the β_{jk} are the regression coefficients to be estimated. The random effects ε^{R}_{ij}, $\varepsilon^{P}_{P(i)j}$ and $\varepsilon^{F}_{F(i)j}$ model variation in species occurrences and co-occurrences at the

resource unit (R), plot (P) and forest site (F) levels. The indices P(i) and F(i) denote the plot and the forest site to which the resource unit i belongs, respectively. We assume that these effects are distributed according to the multivariate normal distributions $\varepsilon^R_{i\cdot} \sim N(0,\Omega^R)$, $\varepsilon^P_{P\cdot} \sim N(0,\Omega^P)$ and $\varepsilon^F_{F\cdot} \sim N(0,\Omega^F)$, where Ω^R, Ω^P and Ω^F are species-to-species variance–covariance matrices. The residual term $\in_{ij} \sim N(0,1)$ corresponds to the probit link function which is needed to convert the linear scale into a probability scale. As detailed in Ovaskainen et al. (2016), the model was fitted to the data using a Bayesian latent variable approach that enables the estimation of the high-dimensional variance–covariance matrices.

We characterized the positions of the species within the interactive networks by four association measures, all derived from the total species-to-species covariance matrix $\Omega = \Omega^R + \Omega^P + \Omega^F$, which measures how much of the occurrences of the species are influenced by the occurrences of the other species at all spatial levels. We inverted and scaled the covariance matrix Ω to yield the partial correlation matrix, which we denote by R. We derived the association measures from the partial correlation matrix R instead of the covariance matrix Ω, as the latter is influenced also by indirect links among the species and thus less likely to characterize causal links than the partial correlation matrix (Ovaskainen et al. 2016). Our first association measure consists of the sum of squared partial correlations over the other species, computed for species j as $A_j = \sum_{k\neq j} R^2_{kj}$. This measure describes how strongly the species j is associated to the occurrences of all other species. Our second and third measures are $A^+_j = \sum_{k\neq j, R_{kj>0}} R^2_{kj}$ and $A^-_j = \sum_{k\neq j, R_{kj<0}} R^2_{kj}$, which are the sums of the positive A^+_j and negative A^-_j squared partial correlations, respectively. These measures differentiate species for which the associations are primarily negative (or antagonistic) from species for which the associations are primarily positive (or facilitative).

Finally, our fourth measure A^*_j differentiates species which have many weak links to other species from species which have few strong links to other species. To compute A^*_j, we define species that are linked to species j as those species for which the partial correlation with species j is positive or negative with at least 95% posterior probability. For all species with at least one linked species, we computed the mean link strength as the average squared partial correlation among the linked species. We then classified the species to two groups as follows. We considered that a species had many weak links ($A^*_j = -1$) if the number of links was at least 10 and the mean link strength was smaller than the average over all species. Conversely, we considered that a species had few strong links ($A^*_j = 1$) if the number of links was smaller than 10 and the mean link strength was greater than the average over all species. As we wished to contrast only these two groups, we left A^*_j undefined for the remaining species.

To explore the link between species niches and their positions with the interactive networks, we considered the four association measures A, A^+, A^- and A* as response variables (with A, A^+, A^-log-transformed), which we related to the following four explanatory variables: the commonness of the species (E_1), dependency on large logs (E_2), preferred decay class (E_3), and specificity in decay class (E_4). For commonness we used the log-transformed number of occurrences of the species in the natural forest data. For the dependency on large logs E_2 we used the posterior mean of the regression coefficient β_{j2} that measures how the occurrence probability of species j depends on the volume of the resource unit. We measured the preferred decay class and specificity in decay class by predicting the occurrence probabilities to logs of different decay stages and computing the expectation (E_3) and inverse of the variance (E_4).

To measure the responses of the species to forest management, we considered data from the natural forests as the reference level, and contrasted the observed species abundances in managed forests to three predictions. With prediction 0 we asked how much species abundance (measured as the number of occurrences per unit area of forest) in managed forests differs from the reference level found in natural forests. To generate prediction 0, we computed the mean number of occurrences per plot in the natural forests, and predicted that the species would occur with the same abundance also in managed forests. With prediction 1 we accounted for resource availability, and with prediction 2 we accounted additionally for species-to-species associations. To generate predictions 1 and 2, we used the model fitted to the natural forest data to predict species occurrences on the resource units surveyed in managed forests, either accounting only for the environmental covariates (prediction 1), or additionally on the occurrences (at all spatial scales) of species other than the focal species (prediction 2). For a description of how the latent variable model can be used to generate such predictions, we refer to Ovaskainen et al. (2016). We computed for each species j an index F_j measuring its response to forest management. We defined F_j as the log-transformed ratio between the observed and predicted (by predictions 0, 1 or 2) number of occurrences within managed forests, where the prediction was based on data from natural forests. Thus $F_j > 0$ (respectively, $F_j < 0$) indicates that the species j benefits from (respectively, is harmed by) forest management, as its prevalence in managed forests is higher (respectively, lower) than predicted from its occurrence in natural forests.

To examine the link from species niche to its sensitivity to forest management, we used linear models to relate the response to forest management to the explanatory variables E_1 –E_4. To examine the link from the position of the species within the interaction network to its sensitivity to forest management, we added also the association measures A, A^+, A^- and A*(with A, A^+, A^- log-transformed) as explanatory variables. As response variables in these models, we used either the response to forest management F, or the log of its square log (F^2). While the analyses with F ask which kind of species have declined and which kind of species have increased due to forest management, the analyses with log (F^2) ask which kind of species have generally responded (either positively or negatively) to forest management. As species with tight links to other species and especially mutualistic species have been shown to respond negatively to perturbations (e.g. results from Biesmeijer et al. 2006, Aizen et al. 2012), we expected that F correlates negatively with A, A^+, A^- and A*, and more strongly with A_+ than A^-. As species with strong links to other species are more likely to show indirect effects, we expected that log (F^2) correlates positively with A,A^+ and

A^-. Further, as the effects of few strong links are less likely to balance each other out than the effects of many weak links, we expected that log (F^2) correlates positively with A*.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.48636> (Abrego et al. 2016b).

Results

The association measures A^+ and A^- were positively correlated with each other (correlation coefficient for log-transformed values 0.88), indicating that species with strong negative associations also have strong positive associations. Consequently, the overall measure A was highly correlated with its positive and negative components (for log transformed values, correlation coefficient between A and A^+ 0.97, and between A and A^- 0.97). All three association measures A, A^+, A^- increased with the commonness of the species E_1 ($p = 0.003$ for A; $p = 0.001$ for A^+; $p = 0.02$ for A^-) but they did not co-vary with the covariates related to the species niche E_2–E_4 ($p > 0.05$ for all cases). The measure A* did not co-vary with any of the covariates E_1–E_4 ($p > 0.05$ for all cases). Thus, common species were more strongly linked to other species than rare species, but the association measures provided an independent axis from the species niche.

Those species that were common in natural forests were generally common also in managed forests, as shown by the positive regression slope in Fig. 1A. Species abundances, measured as mean number of occurrences per plot, were lower in managed forests than predicted from their abundances in natural forests (Fig. 1A) for 88 out of the 98 species. For the median species, the abundance in managed forests was 34% of that in the natural forests. The generally lower abundances in managed forests were explained by lower resource availability: when accounting for resource availability in managed forests, the predicted level of species abundance matched well with the observed abundances (Fig. 1D). The model's ability to predict which species were rare and which common in managed forests improved further when accounting for species-to-species associations (Fig. 1G).

Based on prediction 0, the response to forest management F was negative for most species, and especially negative for those species that were common in natural forests (E_1, $p = 0.02$), that preferred large resource units (E_2, $p < 0.001$) and late decay stages (E_3, $p < 0.001$). Additionally, the response to forest management decreased with increasing association measures A ($p = 0.009$, Fig. 1B), A^+ ($p = 0.008$) and A^- ($p = 0.02$), but it did not co-vary with the association measure A* ($p > 0.05$). Thus, especially those species which have tight associations with other species have declined as a response to forest management. As an example illustrating this result, *Biscogniauxia nummularia* had a high association index A, and showed a negative response

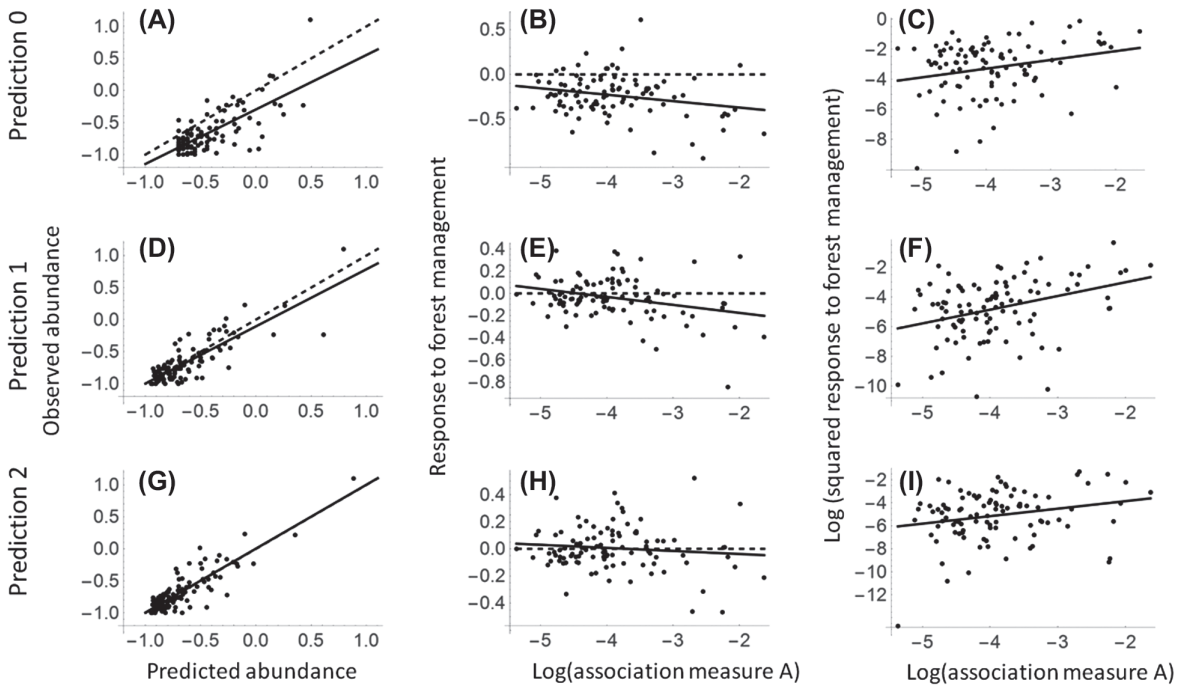

Figure 1. The responses of species to forest management explained by resource availability and species-to-species associations. The left-hand panels (ADG) show the log(n + 0.1) transformed mean number of species occurrences in a 10×10 m plot in managed forests against three predictions based on data from natural forests: observed abundance per plot (prediction 0) and predictions that account for environmental variables (prediction 1) and additionally for occurrences of other species (prediction 2). The dashed lines show the identity $y = x$, and the continuous lines linear regressions, the R^2-values of which are 0.52 (panel A), 0.69 (C) and 0.75 (E). In the middle panels (BEH) and in the right-hand panels (CFI), the responses to forest management (true abundance minus predicted abundance) have been regressed against the log-transformed association index A and its square, respectively.

to forest management, whereas *Fuscoporia ferruginosa* had a low association index A, and showed a positive response to forest management (see Supplementary material Appendix A1 for species-specific results). As for prediction 0 most of the responses to forest management were negative, the results for log (F^2) were not independent but they basically reflected those obtained for F. Thus, log(F^2) increased with E_1 ($p = 0.04$) and E_2 ($p < 0.001$), and it increased with the association measures A ($p = 0.04$, Fig. 1C), A^+ ($p = 0.03$) and A^- ($p = 0.08$). Unlike F, the response variable and log (F^2) increased with A* ($p = 0.04$), suggesting that species with few strong links showed in general stronger responses to forest management than species with many weak links.

After accounting for the availability of resources in managed forests (prediction 1), the response to forest management F was not influenced by any of the covariates E_1–E_4, it decreased with the association measures A ($p < 0.001$, Fig. 1E), A^+ ($p = 0.002$) and A^- ($p < 0.001$), and did not co-vary with A* ($p > 0.05$). The squared response log (F^2) was not influenced by any of the covariates E_1–E_4, it increased with the association measures A ($p = 0.001$, Fig. 1F), A^+ ($p = 0.002$) and A^- ($p = 0.003$), and did not co-vary with A* ($p > 0.05$). Thus, also after accounting for the reduced resource availability in managed forests, species with tight associations with other species showed stronger and on average more negative responses to forest management than species not tightly linked to other species.

After accounting for the occurrences of the other species in the managed forests (prediction 2), the response to forest management was not explained by any of the covariates E_1–E_4 nor the association measures A, A^+, A^- or A* ($p > 0.05$), the negative results holding both for F and for log(F^2) (Fig. 1HI).

The species specific results for the responses of the species to forest management (based on predictions 0, 1 and 2), explanatory variables (E_1–E_4), and association measures (A, A^+, A^-, A*) are given in the Supplementary material Appendix A1.

Discussion

Quantifying networks of ecological interactions and assessing their changes due to global environmental change has been the focus of much recent research (Tylianakis et al. 2008, Araújo et al. 2011). Empirical and theoretical studies on animal–plant mutualistic interactions have demonstrated that loss of individual species can lead to consequences to the other species, such as secondary species extinctions (Borrvall et al. 2000, Biesmeijer et al. 2006, Aizen et al. 2012). However, whether theoretical and empirical results obtained from directly observable networks are generalizable to more cryptic networks has remained as an open question.

We found that in a large community of wood-inhabiting fungal species that involves many kinds of species associations, species that are strongly linked to other species are especially sensitive to forest management, thus supporting the generality of previously reported results. Our results also give support to the earlier finding that the responses of species which have few tight links to other species are more pronounced than of species which have many weak links (Aizen et al. 2012). Nevertheless, our results differ from the prediction that mutualistic networks are more sensitive to disturbances than antagonistic ones (Tylianakis et al. 2008). In our case, species that had positive or negative associations to other species were equally significantly affected by forest management. Therefore, we found the best predictor to be the association measure A which integrates the effects of both positive and negative associations. This difference to earlier results is likely due to the fact that fungal communities involve complex networks of many kinds of direct and indirect interactions. These interactions include e.g. parasitic relationships and facilitation or inhibition of growth through metabolite secretion and modification of the substrate (Heilmann-Clausen and Boddy 2005, Boddy et al. 2008, Pippola and Kotiranta 2008).

While fungal interactions have been tested experimentally in the small scale (Boddy 2000, Heilmann-Clausen and Boddy 2005), a direct and robust measurement of fungal interactive networks is presently not feasible. This is not only due to the high number of species involved, but also due to the differences between laboratory and natural conditions. For this reason, we have taken an alternative methodological approach, namely to use statistical associations as a proxy for ecological interactions. To partition out variation induced by measured environmental conditions, we have not assessed associations from raw data (as e.g. in Ulrich and Gotelli 2010), but from residual variation after accounting for environmental niches (Ovaskainen et al. 2010, Ovaskainen et al. 2016). Still, statistical associations can be considered only as hypotheses on ecological interactions, and their confirmation requires an experimental approach.

In the case of wood-inhabiting fungi, a large body of literature including our previous studies on the same data has demonstrated negative impacts of forest management on species richness and community composition, mainly due to decreasing amount and quality of dead wood in managed forests (Junninen and Komonen 2011, Abrego and Salcedo 2013, 2014, Nordén et al. 2013). Our results give further support to the earlier finding that species that are specialized to large and much decayed logs have declined in particular (Penttilä et al. 2006, Abrego and Salcedo 2013, Nordén et al. 2013). In our results, the species that showed negative responses to forest management depended more on large and decayed resource units than those species that benefited from forest management. However, in our results the generally lower abundances of the species in managed forests was explained by the decline in their resources, whereas in the results of Nordén et al. (2013) specialized species had decreased even more than their resources. The discrepancy between the two results may be due to the fact that the study of Nordén et al. (2013) covered a much larger spatial scale than the present study, and thus the influences of dispersal limitation and habitat fragmentation are expected to be less pronounced in the present case.

Both theoretical and empirical studies have shown that species with specialized resource use are more sensitive to habitat loss and fragmentation than species with generalistic resource use (Henle et al. 2004, Nordén et al. 2013). Here we bring a new dimension by showing that those fungal species which are tightly linked to other species have declined

especially much due to forest management, whereas species with weak associative links have on average become more abundant in managed forest sites than predicted by resource availability. If those species with tight links to other species are regarded as specialists, our result is in line with the earlier findings (Weiner et al. 2014).

Our sampling method consisted of a single fruit body based survey, which compared to molecular surveys or repeated fruit body based surveys detects less species especially at the resource unit level. The reason for conducting a single fruit-body survey in the peak season rather than repeatedly surveying the same dead wood units over time is that the single survey strategy has been shown to be more cost-effective than repeated surveys on the same resource units for deriving ecological inferences, as it provides a larger number of independent data points (Abrego et al. 2016a). A comparison of co-occurrence patterns between molecular surveys and fruit-body surveys could bring additional insights on the mechanisms behind fruiting, especially on the role of competition. However, while molecular surveys have been combined with fruit body surveys at small scale (Ovaskainen et al. 2013, Runnel et al. 2015, Ottosson et al. 2015), conducting a molecular survey at the scale of the present study (consisting of tens of thousands of resource units in tens of study sites) is highly challenging, and thus we consider this as an interesting avenue for future work.

As our results suggest that wood-inhabiting fungal species do not respond independently to forest management effects, cost-effective conservation strategies should be based on community-level rather than species-level approaches. Although some theoretical models predict that species co-extinctions may be one of the most common causes of global biodiversity loss (Koh et al. 2004, Dunn et al. 2009), the effect of interactive associations has been scarcely considered in conservation studies thus far (Pimm and Raven 2000).

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Supplementary material (available online as Appendix oik-03674 at <www.oikosjournal.org/appendix/oik-03674>). Appendix 1. Species specific results for the responses of the species to forest management (prediction 0, 1 and 2), explanatory variables (E_1–E_4), and association measures (A, A^+, A^-, A*).